RELATIONSHIPS OF THE AFRICAN KILLIFISH GENUS FOERSCHICHTHYS (TELEOSTEI: CYPRINODONTIFORMES: APLOCHEILIDAE)

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Abstract.—The genus Foerschichthys was named by Scheel and Romand (1981) for Aplocheilichthys flavipinnis Meinken, a diminutive species of killifish from the Niger Delta. The relationship of this species to other killifishes has been debated since its description. An osteological and external morphological examination reveals that Foerschichthys flavipinnis 1) is an aplocheiloid killifish; 2) is a member of the solely Old World family Aplocheilidae; and 3) is more closely related to the group including Aplocheilus, Pachypanchax and Epiplatys than it is to the group including Aphyosemion, Fundulopanchax and Nothobranchius. Foerschichthys is distinguished from all other aplocheiloid killifishes by the derived placement of the dorsal fin entirely posterior to the anal fin.

Meinken (1929) reported the existence of a new, diminutive killifish species (family Cyprinodontidae *sensu* Myers 1955) from the Niger Delta, referring to it as "*Panchax* species *nov*. der Zwergpanchax," the dwarf or pygmy *Panchax*. As used by Meinken (1929), *Panchax* was a general reference for Old World killifishes of the subfamily Rivulinae Myers (=suborder Aplocheiloidei as defined by Parenti 1981).

Meinken (1932) formally described the new dwarf *Panchax* as *Aplocheilichthys flavipinnis*, thus changing his tentative suprageneric placement of the species from the aplocheiloid killifishes (suborder Aplocheiloidei) to the relatively unrelated aplocheilichthyine killifishes (suborder Cyprinodontoidei, family Poeciliidae, subfamily Aplocheilichthyinae), more commonly known as the lampeyes or the procatopines (see Parenti 1981). Primarily because the aplocheiloids and aplocheilichthyines comprise the subsaharan African killifish fauna, they have often been discussed as close relatives (e.g., Ahl 1924, 1928; Huber 1979; Scheel 1968; Scheel and Romand 1981).

Scheel (1968) claimed that Aplocheilichthys flavipinnis possessed a greater number of aplocheiloid than aplocheilichthyine characters, and suggested that it be referred to as "Aphyosemion" flavipinnis until a more precise statement of relationship of the species could be made. (Aphyosemion is a large genus of primarily West African aplocheiloids.) Scheel believed that the species was more closely related to Aphyosemion than to Epiplatys, which, at that time, was the other African aplocheiloid genus containing several diminutive forms.

Scheel and Romand (1981) compared A. flavipinnis to four species of diminutive killifishes, the African Adamas formosus Huber, Epiplatys duboisi Poll, and E. annulatus (Boulenger), and the South American Fluviphylax pygmaeus (Myers and Carvalho), all of which they considered to be aplocheiloids. Because A. flavipinnis differs from all four species, they named a new genus, Foerschichthys, for the species. They were unable to make a statement concerning the relationship

of the genus other than its being aplocheiloid, and supported their taxonomic decision by stating that (p. 30): ". . . we find ourselves unable to place A. *flavipinnis* in any known rivulin genus."

Parenti (1981) reclassified the killifishes, the order Cyprinodontiformes, into two suborders, the Aplocheiloidei and the Cyprinodontoidei, defining each order as monophyletic (*sensu* Hennig 1966) using derived, primarily osteological, characters. *Fluviphylax pygmaeus* was classified as a cyprinodontoid (in the family Poeciliidae, subfamily Fluviphylacinae), whereas the other species compared by Scheel and Romand (1981) were classified as aplocheiloids. The relationship of *Fluviphylax* to the aplocheilichthyines and the viviparous poeciliids was presented as an unresolved trichotomy by Parenti (1981), and that genus should not be considered an aplocheiloid as it was by Scheel and Romand (1981).

The present investigation was prompted by my own observations and those of Scheel (1968) and Scheel and Romand (1981) that *Foerschichthys* shares with *Fluviphylax pygmaeus* the derived character of the placement of the dorsal fin posterior to the anal fin.

The objectives of the present study were to determine 1) if there are uniquely derived characters to define *Foerschichthys*; 2) if the genus is more closely related to the aplocheiloids or to the cyprinodontoids (including the aplocheilichthyines); and 3) to what genus or group of genera it is most closely related. The possibility that *Foerschichthys* is a close relative of *Fluviphylax* was considered initially and then rejected after an examination of material revealed that *Foerschichthys* is an aplocheiloid killifish.

Discussion

Aplocheiloid and aplocheilichthyine killifishes superficially resemble each other and have often been confused in the literature. The suborder Aplocheiloidei (order Cyprinodontiformes) is defined as monophyletic by nine derived characters (Parenti 1981:374): 1) attached orbital rim; 2) cartilaginous mesethmoid; 3) close-set pelvic girdles; 4) a broad anterior end of basihyal; 5) a narrow and twisted preorbital bone; 6) tubular anterior naris; 7) reduced cephalic sensory pore pattern; 8) males more elaborately pigmented than females; and 9) posterior extension of vomer dorsal to anterior ramus of parasphenoid. The genera *Foerschichthys, Adamas, Aphyosemion* and *Epiplatys* are members of the suborder Aplocheiloidei.

Although some of these characters appear in the suborder Cyprinodontoidei, their occurrence in that suborder has been most parsimoniously assessed as homoplasious by Parenti (1981). Twelve derived characters were given to define the suborder Cyprinodontoidei as monophyletic (Parenti 1981:403–404). These include two rather than three ossified basibranchials, and the absence of the dorsal hypohyal, the metapterygoid, the first dorsal fin ray, as well as several upper jaw ligaments. Aplocheilichthyine killifishes, as well as *Fluviphylax pygmaeus*, are members of the suborder Cyprinodontoidei.

Within the Aplocheiloidei, there are two families, the Old World Aplocheilidae and the New World Rivulidae. The Aplocheilidae is defined as monophyletic by four derived characters (Parenti 1981:387): 1) supracleithrum fused to posttemporal; 2) basihyal a small triangular bone capped by a large wedge of cartilage;

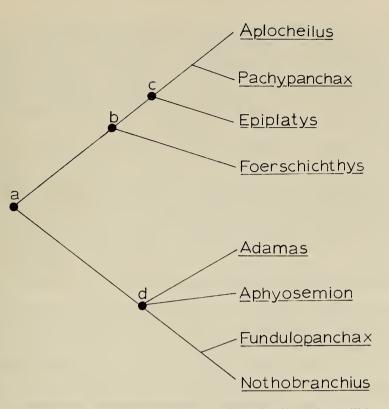


Fig. 1. Cladogram of relationships of the genera of the family Aplocheilidae. Derived characters at each lettered node are as below. For characters defining other nodes, and a discussion of relationships of genera and their included subgenera, see Parenti (1981). a. Posttemporal fused to supracleithrum; reduction of ossified section of basihyal to a small, triangular wedge; interarcual cartilage attaches directly to the articulation point of the second pharyngobranchial; premaxillary processes tapered posteriorly. b. Reduction of the uncinate process on the fourth epibranchial; premaxillary ascending processes expanded. c. Expanded coronoid process on the dentary; bifurcate dorsal hypural plate in juveniles and some adults; absence of the uncinate process of the fourth epibranchial. d. Bifid epipleural ribs; attenuate posterior extension of the vomer.

3) premaxillary ascending processes tapered posteriorly; and 4) interarcual cartilage attaching directly to articulation point of second pharyngobranchial. *Foerschichthys, Adamas, Aphyosemion* and *Epiplatys* are members of the Aplocheilidae.

The family was divided informally into two groups that were not named as subfamilies by Parenti (1981) because the distinction among species of the most primitive genera of each group is problematic. However, *Foerschichthys* possesses two of the defining characters of the *Aplocheilus-Pachypanchax-Epiplatys* group (Parenti 1981:395). The premaxillary ascending processes are relatively expanded, although not as greatly as in *Aplocheilus panchax* (Parenti 1981:359, Fig. 4a), rather than being attenuate as in *Aphyosemion petersi* (Fig. 4c). Also, in *Aplocheilus panchax* (Parenti 1981:388, Fig. 24a) there is no uncinate process on the fourth epibranchial, and therefore the fourth epibranchial is not in contact with the third. In *Foerschichthys* the uncinate process of the fourth epibranchial is reduced, with a cartilaginous cap for articulation with the uncinate process of the third epibranchial. The relationships of the major groups of aplocheiloid genera are summarized in Fig. 1. A clearer statement of the relationships among all nominal aplocheiloid genera and subgenera awaits a revision of all included species.

Scheel and Romand (1981) defined *Foerschichthys* phenetically, stating that it differed from other African aplocheiloids (of which group they considered *Fluviphylax* to be a member) by a combination of three characters: 1) pigmentation pattern; 2) karyotype; and 3) origin of the dorsal fin. Only the state of the last character was analyzed in terms of being primitive or derived, and it is the only derived character by which the genus is defined.

The pigmentation pattern is characterized by a narrow, black median line, and a similar black line along the base of the anal fin. Such a pigmentation pattern characterizes many atherinomorph fishes (the larger group to which cyprinodontiforms belong) and is commonly found in aplocheilichthyines among the cyprinodontiforms. Because of its wide distribution, the pigmentation pattern should initially be assessed as primitive for atherinomorph fishes. However, considering that, as listed above, a defining character of the suborder Aplocheiloidei is that males are more elaborately pigmented than females, the much less elaborate pattern of Foerschichthys is perhaps secondarily derived. As stated by Scheel and Romand (1981:23): "Such narrow black lines occur in almost all juveniles and adult procatopodin [aplocheilichthyine] species but are very rare in rivulin [aplocheiloid] fish; they have been observed only in Epiplatys annulatus and in the two Asian fishes Aplocheilus blocki (Arnold, 1911) and A. panchax (Hamilton-Buchanan, 1822), but in these fishes the lines disappear with age." Thus, if the pattern is considered secondarily derived, it further supports the alignment of Foerschichthys with the Aplocheilus-Pachypanchax-Epiplatys group.

The general number of haploid chromosomes in teleost fish is 24. Fishes of the *Aphyosemion-Nothobranchius* group typically have a very low haploid chromosome number; the lowest number reported is nine (Scheel 1968). *Foerschichthys flavipinnis* has a haploid chromosome number of 20 which Scheel and Romand (1981) point out as a character that distinguishes it from the other diminutive aplocheiloids. However, it is not a unique karyotype for aplocheiloid fishes. Furthermore, given that the haploid chromosome number ranges from nine to 25 in cyprinodontiforms, the karyotype of *Foerschichthys* may simply represent a stage in a transition series from a high to a low chromosome number.

The only derived character defining *Foerschichthys* within the aplocheiloids is the placement of the dorsal fin posterior to the anal fin. *Fluviphylax pygmaeus* shares this character but is closely related to the aplocheilichthyine cyprinodontoids. The occurrence of this character in both genera indicates that it is independently and secondarily derived.

The description that follows is based on personal observation as well as data from Meinken (1932), Scheel (1968) and Scheel and Romand (1981). The characters and their order are similar to those given for other cyprinodontiform genera by Parenti (1981).

Foerschichthys Scheel and Romand

Foerschichthys Scheel and Romand, 1981:30, type by original designation Aplocheilichthys flavipinnis Meinken.

Diagnosis.—Distinguished from all other aplocheiloid killifishes by having the dorsal fin situated entirely posterior to the anal fin.

Foerschichthys flavipinnis (Meinken)

"Panchax species nov." Meinken, 1929:385, aquarium description.

Aplocheilichthys flavipinnis Meinken, 1932:54, original description, Nigeria, Lagos.—Kaden, 1967:280, aquarium description, color pattern.—Foersch, 1968: 142–143, aquarium description.—Scheel, 1968:211–214, discussion of relationships.

"Aphyosemion" flavipinnis Scheel, 1968:214, tentative referral of this species to Aphyosemion.

Foerschichthys flavipinnis Scheel and Romand, 1981:30, proposal of a new genus with A. flavipinnis as its type. Combination "Foerschichthys flavipinnis" used only in figures on pages 24 and 25, and table on page 26.

Diagnosis.—Same as for genus.

Description.—Anal: iv, 10; Dorsal: ii, 6; Pelvic: 6; Pectoral: 13; Vertebrae: 13 + 17; Scales in lateral series: 30–31.

First pleural rib on parapophysis of second vertebra; parapophysis not reduced; no pleural rib on the first hemal spine; hypural plates fused into an hypural fan. Epipleural ribs not bifid.

Anal fin not modified into a gonopodium; anal fin musculature unmodified; first proximal radial present; middle anal radials present.

One dorsal fin ray articulating with each of first two dorsal radials; dorsal fin origin posterior to anal fin.

Autopterotic fossa normal; lateral ethmoid not expanded medially, not reaching parasphenoid; parasphenoid not expanded anteriorly; weakly formed supraoccipital and epiotic processes; neural spine on first vertebra; first vertebra articulates with skull via basioccipital and exoccipital condyles; supraoccipital excluded from formation of foramen magnum; parietals present; nasals not expanded medially.

Mesethemoid cartilaginous; medial process of pelvic fin base and ischial process reduced; interarcual cartilage attached directly to articulation point of second pharyngobranchial; basihyal broad anteriorly, small triangular ossification posteriorly; no tooth patches on second and third hypobranchials; few teeth on fourth ceratobranchials; dorsal and ventral hypohyal present; anterior extension of anterior ceratohyal ventral to hypohyals; reduced uncinate process on fourth epibranchial articulates with that of third; first epibranchial narrow at its base. Interhyal ossified; three ossified basibranchials. Vomer with posterior extension dorsal to parasphenoid.

Preorbital bone narrow and twisted, carrying distinct sensory canal; dermosphenotic and preopercle with distinct sensory canal; pectoral girdle lowset; first postcleithrum present; posttemporal straight, with ligamentous ventral limb; posttemporal fused to supracleithrum.

Vomer present, edentulous; medial ramus of maxilla twisted with no pronounced dorsal process, ventral process gently curved toward and abutting rostral cartilage, lateral ramus narrow.

Premaxillary ascending processes flat and broad, slightly tapered posteriorly, not overlapping in the midline; rostral cartilage large; lateral ramus of premaxilla with alveolar process not indented posteriorly. Ligament extending from ventral processes of maxillae to middle of rostral cartilage; ethmomaxillary ligament present; meniscus present between premaxilla and maxilla. Dentary not expanded medially, not robust; coronoid process on dentary not overlapping that of angulo-articular; retroarticular not elongate. Autopalatine with straight head, ventral process not elongate, not reaching quadrate; metapterygoid reduced.

Orbital rim attached; anterior naris tubular; supraorbital sensory pores reduced to a series of neuromasts situated in open troughs; preopercular and mandibular canals open troughs; two preorbital pores.

Males larger than females. Pigmentation pattern: thin median black line, thin black line on base of anal, males with scales above median black line edged in red; dorsal and anal fins yellow to orange, males with light blue fin edges; no spot at anterior base of dorsal fin; throat bars present.

No fatty predorsal ridge; caudal fin scaled for approximately one-third its length; caudal fin with a single, median posterior point; swimbladder extends posteriorly to first hemal spine.

Distribution.—Known from following Nigerian localities: Ibefun, south of Ijebu-Ode; Ughelli, east of Warri of the Niger Delta; Aduna, about 67 km south of Isela-Ubu; Auna, between Ijebu-Ode and Shagamu; Aiyetoto (Scheel 1968).

Remarks.—Meinken (1932:53) stated that the types of *Aplocheilichthys flavipinnis* were to be deposited in the Berliner Zoologische Museum, but a search of the collection by Dr. H.-J. Paepke failed to locate them. Nevertheless, a neotype will not be designated at this time, following the recommendations of the International Code of Zoological Nomenclature, because it is possible that the type material is mislabelled in the Berlin Museum or is at another institution.

Material Examined

Foerschichthys flavipinnis: Nigeria: Niger Delta at Ughelli: MCZ 49881 (4 spec., 1 specimen counterstained with alcian blue and alizarin red S).

Fluviphylax pygmaeus: Brazil: Manaus: MCZ 46712 (21 spec.); MCZ 46713 (64 spec., 3 spec. counterstained); MCZ 46714 (11 spec.); MCZ 49958 (14 spec., 4 spec. cleared and alizarin stained); Lago Hyanuary: MCZ 41367 (5 spec.); Rio Madeira at Borba: SU 50196 (3 spec.) Paratypes.

Adamas formosus: Zaire: Village of Ntokon near the banks of the Likouala-Mossaka: MNHN 1979–199 (1 spec.) Holotype.

Epiplatys annulatus: Sierra Leone: BMNH 1914.12.9:5–6 (2 spec.). Syntypes. Additional comparative data were taken from Parenti (1981).

Summary

The monotypic African killifish genus *Foerschichthys* was named by Scheel and Romand (1981) for the diminutive *Aplocheilichthys flavipinnis* Meinken because they could not place it in any of the known tropical killifish genera with dwarf forms (*Aphyosemion, Adamas, and Epiplatys* of Africa and *Fluviphylax* of South America). *Foerschichthys* is distinguished from all other aplocheiloid genera by having the dorsal fin situated entirely posterior to the anal fin.

An examination of osteological and other anatomical features of *Foerschichthys flavipinnis* reveals that it does not possess the derived features of the suborder Cyprinodontoidei, the group in which *Fluviphylax* is placed (Parenti 1981), but that it possesses the derived features of the suborder Aplocheiloidei. *Foerschich*-

thys may be considered a primitive member of the Aplocheilus-Pachypanchax-Epiplatys group of the family Aplocheilidae.

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